

## Ocean current variability and the spawning season of Hawaiian reef fishes

Phillip S. Lobel

Woods Hole Oceanographic Institution, Woods Hole, MA 02543, U.S.A.

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### Synopsis

The spawning patterns of four Hawaiian reef fishes with similar reproductive habits, but different biogeographic distributions were studied from September 1980 to October 1981. Two species are Hawaiian endemics [*Centropyge potteri* (Pomacanthidae) and *Chaetodon multicinctus* (Chaetodontidae)] and the other two have pan-tropical Pacific distributions [*Ctenochaetus strigosus* and *Zebrasoma flavescens* (Acanthuridae)]. All showed increased spawning activity from January to July, the prevalent pattern among a majority of coastal marine fishes in Hawaii. Environmental correlates to the period of peak reproduction include cycles of (a) daylight length and temperature which probably function as proximate cues and (b) seasonal variations in ocean current patterns which may ultimately affect survival of larvae and dispersal. Peak reproduction takes place during months when (1) mesoscale eddies most likely occur, and (2) the probability is greatest of drifting objects remaining near the islands.

### Introduction

The spawning season for coastal marine fishes in Hawaiian waters extends throughout the year for many species, but most exhibit significantly increased reproduction between February and June (Watson & Leis 1974, Lobel 1978, Walsh 1987).

Recently, Walsh (1987) reviewed possible environmental correlations with the reproductive peak in Hawaii. These variables included photoperiod cycle, water temperature cycle, fluctuating adult food supplies, ocean currents, primary productivity, and ocean salinity. Walsh (1987) argued that water temperatures or photoperiod were the important factors controlling reproduction, and that existing historical data did not support other correlations.

These variables are separable into proximate causal factors (i.e., directly cueing adult fishes) and ultimate causal factors (i.e., developed by natural

selection acting on survivorship and recruitment of larvae). It is possible for several of these variables to be correlated and to have a combined effect on the seasonality of fish reproduction in Hawaii. Although proximate causal factors such as temperature and light cycles are undoubtedly important and are correlated with the peak spawning season, the role of ocean currents and advection of larvae may also be significant and should not yet be dismissed.

In this study, I examined the annual reproductive season of four Hawaiian fishes with similar reproductive styles but different biogeographic distributions. Two of these fishes were endemic Hawaiian species [*Centropyge potteri* (Pomacanthidae) and *Chaetodon multicinctus* (Chaetodontidae)] and two were species with pan-tropical Pacific distributions, [*Ctenochaetus strigosus* and *Zebrasoma flavescens* (Acanthuridae)]. The question was if a defined spawning season was the same

for species of different biogeographical limits. Data from two physical oceanographic studies (Barkley et al. 1964, Patzert 1969) were reanalyzed to evaluate the probability of propagule loss from the islands and the presence of mesoscale ocean eddies during different seasons. The hypothesis tested was that the number of drifters retained around the Islands would be greatest during the coinciding seasons of increased fish spawning activity and ocean eddy occurrence.

### Study site

All fish were collected from coral reefs located between Kailua-Kona and Keahou bays, along the west (Kona) coast of the Island of Hawaii. Reefs ranged in depth from 8 to 20 m. Hobson (1974) described Kona coast reefs and fishes.

Direct observation of fishes was on the Kamoā Reef site, also located about midway between Kailua-Kona and Keahou bays. This site was also a physical oceanographic station at which a current meter and several current drogues were deployed (see Lobel & Robinson 1986, Robinson & Lobel 1985).

### Methods

#### *Gonosomatic index*

The gonosomatic index (GSI) is defined as the ratio of fish gonad weight to body weight. Specimens were collected by spear between 1200 and 1700 h. The purpose for collecting fishes only a few hours before the diel spawning period was to sample ovaries which would have been hydrated by this time, if spawning were to occur on a given date. This procedure provided consistency in gonad status. Specimens were kept on brine-ice until dissected within 48 h. Samples of all four species were collected on the same dates. Collections ( $N = 32$ ) were made from September 1980 to October 1981. The standard length (SL) of specimens was measured in mm.

#### *Gonad and fat weights in *Ctenochaetus strigosus**

Acanthurids of the genus *Ctenochaetus* possess a specialized fat body connected to the gonad (Fishelson et al. 1985). This fat body was dissected from specimens and its ratio to body weight was calculated in the same way as GSI. The ratio of fat to body weight is termed the lipidsomatic index.

#### *Underwater observations*

Approximately 400 scuba dives were performed by the author in the study area at all times of day and night. Fifty-two dives were conducted at one site (Kamoā Reef) during the evening twilight period (approximately 1730 to 1915 h). All observations of reef fishes spawning reported here, were made during this evening twilight period at Kamoā Reef.

#### *Historical data analysis: drift bottles*

Thousands of drift bottles and cards were deployed throughout the central Pacific Ocean between 1960–1963 by the Bureau of Commercial Fisheries in Honolulu. These data (Barkley et al. 1964) recorded locations of deployments and recoveries and calculated probable trajectories. The drifters were weighted to float just beneath the surface. Their drift bottle data were reanalyzed to examine only the proportion of recoveries originating from releases near the Hawaiian islands. A margin of 60 km was selected as a balance between (1) having a significant number of data and, (2) being close enough to the islands to grossly represent the advection of the spawn of reef animals. Data were analyzed for two regions. The first region encompassed the island of Oahu ( $20^{\circ}$  to  $22^{\circ}$  N and  $157^{\circ}$  to  $159^{\circ}$  W). The second region included the major Hawaiian islands. Eighty percent of all drift-bottles released within 60 km of the islands were released within the Oahu region (see below).

## Results

### Annual spawning season

The use of the gonosomatic index as an indication of gonad development, conceals the fact that several discrete processes are taking place in the gonad; it is a crude measure at best. The GSI is of value only in cases where a narrow size range of individuals is sampled (Scott 1979). In cases where the fish sampled vary in size by more than one body length, the GSI is not always the best index (e.g., de Vlaming et al. 1982). The coefficients of variation in the standard lengths of fishes sampled in this study were less than 17% (i.e., less than 1/5 of the body length, Table 1). Specimens were collected within a few hours prior to the dusk spawning period. This provided consistency in ovary status, wherein the eggs became hydrated a few hours before mating. In addition to GSI, corroborative evidence in the literature of gonad histology and recruitment patterns are used to describe spawning seasons. Corroborative evidence is also given in this Results section.

*Centropyge potteri* female GSI data showed maximum gonad weight from March until August (Fig. 1). Males did not exhibit distinct annual variation. This pattern for *C. potteri* from the island of Hawaii in 1980–1981 was similar to *C. potteri* off the island of Oahu in 1973–1975 (see Lobel 1978).

*Chaetodon multicinctus* female GSI data showed a distinct increase in gonad weight in March through June (Fig. 2). Males also showed a broad maximum during this same period. Tricas & Hira-

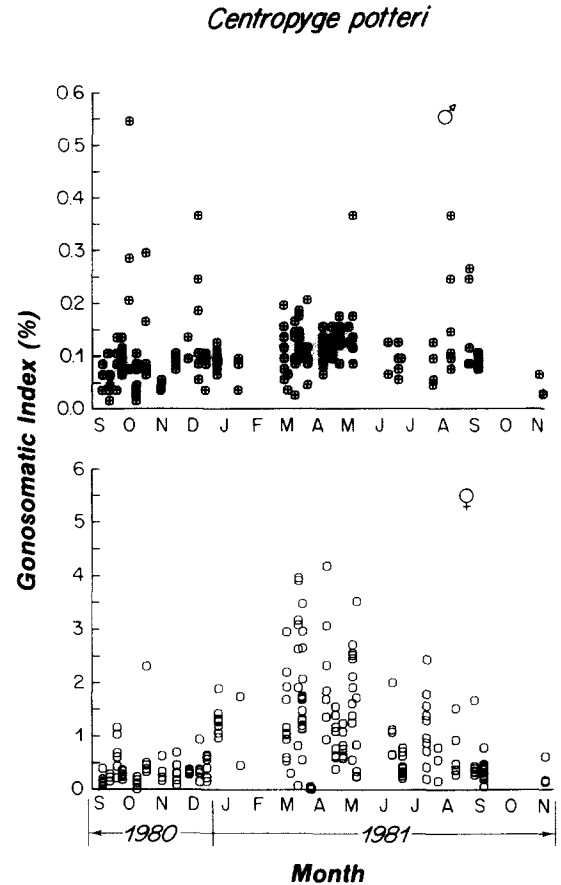


Fig. 1. *Centropyge potteri* (Pomacanthidae) gonosomatic index for males (N = 163) and females (N = 200).

moto (1988) performed a detailed analysis of the gonad developmental histology of this species. Their study spanned an 18 month period during 1981–1982 on Oahu. They concluded that *C. multi-*

Table 1. Coefficient of variation in sizes (SL, mm) of fishes sampled for gonosomatic index measurement.

Species	Sex	N	Mean	± SD	Range		C.V.
<i>Centropyge potteri</i>	Male	163	67	7	54	85	10.8%
	Female	200	58	6	45	77	10.4%
<i>Chaetodon multicinctus</i>	Male	200	67	6	47	89	9.6%
	Female	200	67	6	47	82	8.9%
<i>Ctenochaetus strigosus</i>	Male	160	90	9	66	122	10.3%
	Female	101	81	10	56	101	11.9%
<i>Zebrasoma flavescens</i>	Male	121	100	16	71	137	15.5%
	Female	116	84	14	60	126	16.4%

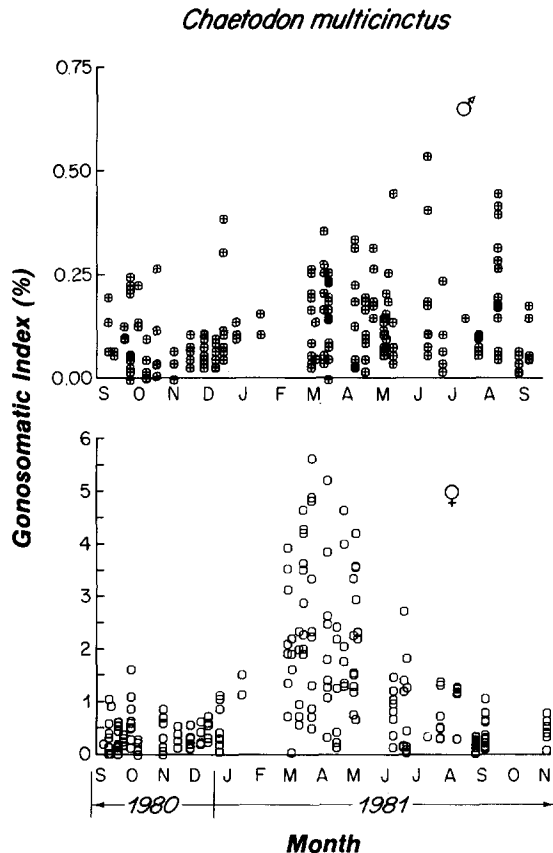


Fig. 2. *Chaetodon multicinctus* (Chaetodontidae) gonosomatic index for males (N = 200) and females (N = 200).

*cinctus* reproductive activity peaked in March, followed by a decline in summer. They also determined that at least some individual fish spawn at all times of the year. They found, however, that the proportion of females spawning during the months of January–July (42%) was greater than females sampled in August–December (15%). Spawning activity was histologically identified by the maturation and hydration of fully yolked oocytes, and postovulatory follicles (Tricas & Hiramoto 1988). Their histological analysis corroborates the spawning pattern suggested by the annual variation in GSI. This activity pattern was also evident in the spawning behavior of wild fish (Lobel 1988). Recruitment of *C. multicinctus* onto Kona reefs was greatest during the summer months (Walsh 1987) which further corroborates a spring spawning peak.

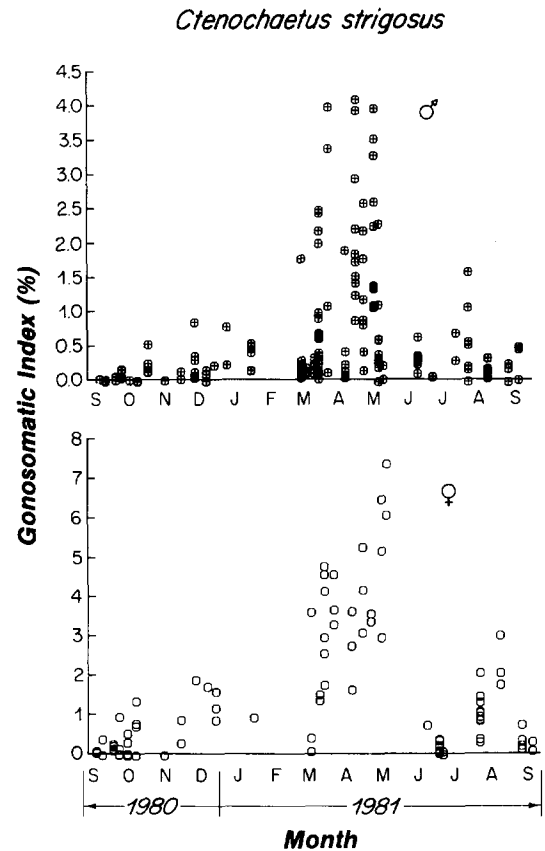


Fig. 3. *Ctenochaetus strigosus* (Acanthuridae) gonosomatic index for males (N = 160) and females (N = 101).

*Ctenochaetus strigosus* male and female GSI data showed distinct maxima in gonad weights from March until June, with a second lesser increase in July–August (Fig. 3). The relative weight of the gonad associated fat body decreased with increased gonad weight (Fig. 4). Histological analyses by Fishelson et al. (1985) suggest that this fat body supports the active gonad during the spawning season. The role of lipid reserves associated with gonad development is a well-known feature in many fishes (e.g. Guillemot et al. 1985). Recruitment of juvenile *C. strigosus* onto Kona reefs occurred mostly during the summer months (Walsh 1987) and corroborates a spring spawning peak.

*Zebrasoma flavescens* male and female GSI data showed heavier gonad weights from March to September (Fig. 5). A gonad-associated fat body was not found in this acanthurid. Maximum recruit-

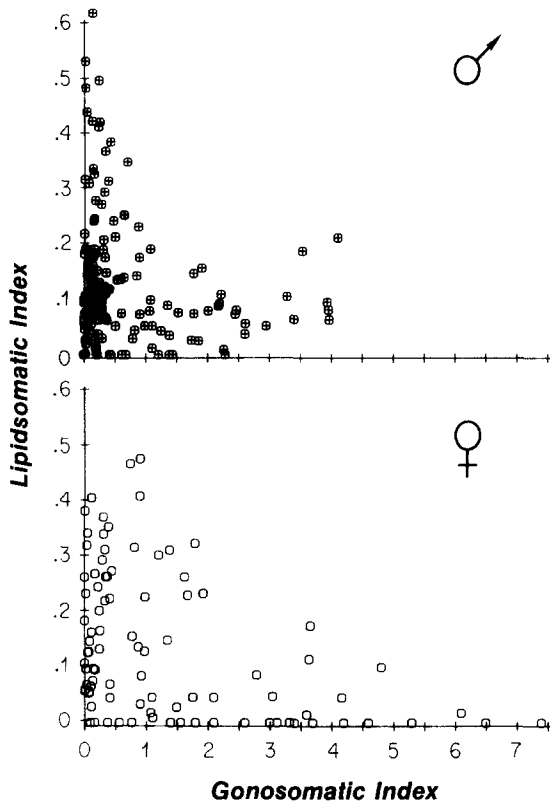


Fig. 4. *Ctenochaetus strigosus*. Relationship between the weight of gonad-connected fat body (lipidsomatic index) and the gonad weight (gonosomatic index) for males (N = 156) and females (N = 92).

ment of juvenile *Z. flavescens* onto Kona reefs occurred during the summer months (Walsh 1987) and corroborates a spring spawning peak.

Underwater observations of fishes at a single site revealed that at least a few individuals of *C. potteri*, *C. multicinctus*, *C. strigosus* and *Z. flavescens* can be found spawning during any time of the year (Table 2). The same conclusion was derived by Tricas & Hiramoto (1988) for *C. multicinctus* based upon gonad histology. Although I had difficulty in obtaining consistent quantitative data on spawning activity (due to water conditions and other variables), it was apparent that overall spawning activity was intense among many individuals from March to August and occasional among few individuals in the late fall-winter. A review of the literature on Hawaiian fishes spawning patterns substantiates

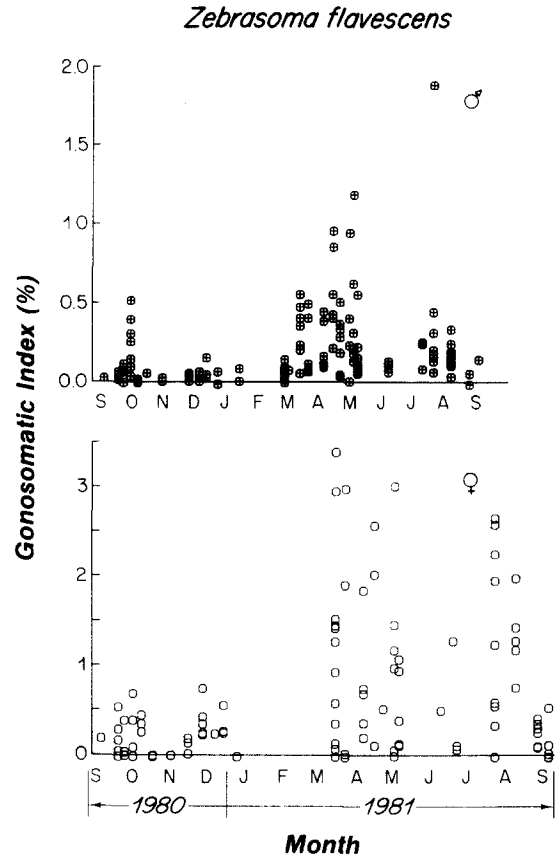


Fig. 5. *Zebrasoma flavescens* (Acanthuridae) gonosomatic index for males (N = 121) and females (N = 116).

this generalization (Walsh 1987).

#### *Ocean current drift*

Drift-bottles and cards which were deployed offshore were picked up by beachcombers who then returned a postcard (Barkley et al. 1964). Thus, these data show the incidence of recovery of drift-bottles found on island beaches and returned to the Fisheries Service. We assume that the return by beachcombers was consistent throughout the years.

The greatest percentage of drift-bottles was recovered on island shores during April–May (Table 3). The percentage return on all Hawaiian islands from January through May was 10.5% compared to

3.9% during June through December (Table 3, Fig. 6). For analysis of long range dispersal of these drifters from the central Pacific see Barkley et al. (1964) and Scheltema (1986).

The locations of 33 mesoscale eddies found in Hawaiian waters were reported by Patzert (1969). These eddies were identified from hydrographic data taken aboard scientific and fisheries research

Table 2. Checklist of fishes seen spawning at Kamoia Reef during the evening period (about 60 minutes before and including sunset).

	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
(number of dives):	(2)	(2)	(13)	(6)	(7)	(0)	(6)	(3)	(1)	(6)	(3)	(2)
Acanthuridae												
<i>Acanthurus achilles</i>			★									
<i>A. nigrofuscus</i>							★					
<i>A. nigroris</i>							★			★		
<i>A. thompsoni</i>			★		★							
<i>Ctenochaetus strigosus</i>	★	★	★	★	★		★	★		★		★
<i>Zebрасoma flavescens</i>	★	★	★	★	★		★	★			★	
Chaetodontidae												
<i>Chaetodon lunula</i>												★
<i>C. multinctus</i>	★		★	★	★		★					
<i>Forcipiger flavissimus</i>							★					
Cirrhitidae												
<i>Paracirrhites arcuatus</i>					★			★		★		
<i>P. fosteri</i>				★								
Labridae												
<i>Pseudocheilinus tetrataenia</i>	★		★	★	★		★					
<i>Stethojulis balteatus</i>												★
<i>Thalassoma duperrey</i>												★
Mullidae												
<i>Parupeneus multifasciatus</i>			★		★		★					
Ostracidae												
<i>Ostracion meleagris</i>			★									
Pomacanthidae												
<i>Centropyge potteri</i>	★	★	★	★	★		★	★		★		
Total species seen spawning	5	3	9	6	8		9	4	0	5	1	4

★ = seen once this month.

★ = seen on two or more dates.

Table 3. Drift-bottle returns to Hawaiian shores when released within 60 km of the islands (data from Barkley et al. 1964).

Date	Hawaiian Archipelago				Around Oahu only			
	Total no. released	Total no. recovered	% recovered/ released	Combined %	Total no. released	Total no. recovered	% recovered/ released	Combined %
Jan-March	955	39	4.1	6.0	600	32	5.3	10.5
April-May	2087	142	6.8		1057	142	10.5	
June-July	8420	310	3.7	3.5	7790	301	3.9	3.9
Aug-Dec	540	12	2.2		210	12	5.5	

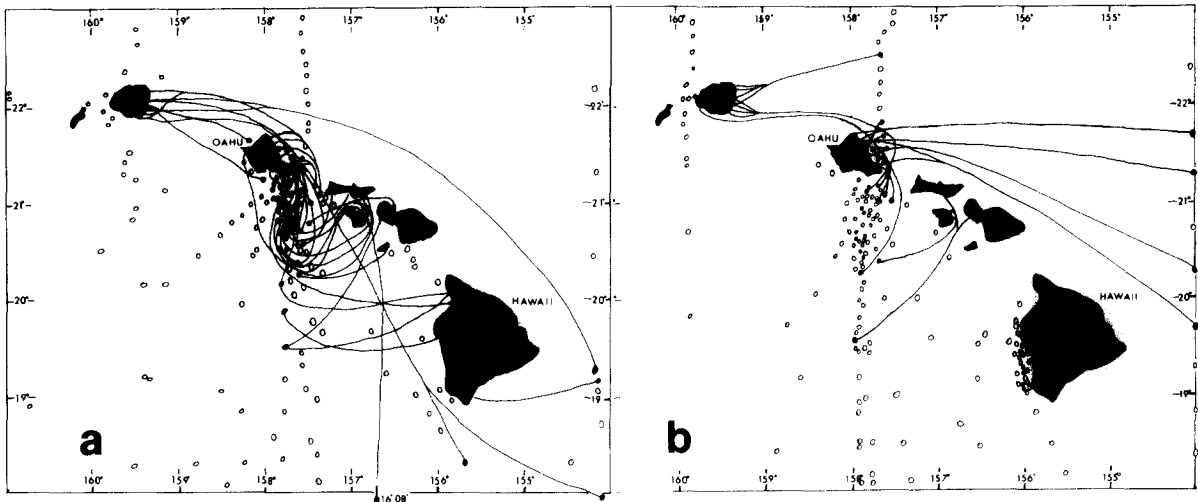


Fig. 6. Drift-bottle deployments, recoveries and inferred trajectories. Open circles are sites of releases but no recoveries. Solid circles are sites of releases with inferred trajectory to recovery location. (a) January through May, and (b) June through December. The release points on  $154^{\circ}$  W indicate progression of current shift in June (Barkley et al. 1964). See Table 3.

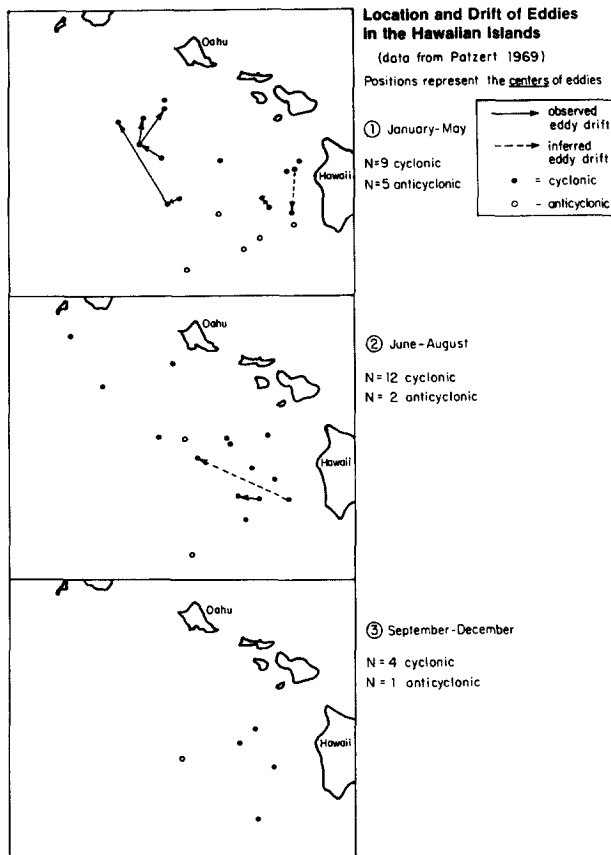


Fig. 7. Historical oceanographic data on the location and drift of mesoscale eddies in Hawaiian waters. Data from Patzert (1969).

vessels from December 1949 to June 1967. Overall, cyclonic eddies outnumbered anticyclonic eddies 3:1. The fewest numbers of eddies were documented from September to December (Fig. 7). The highest percentage of eddy occurrence coincided with the peak period of fish reproduction.

## Discussion

### Seasonal reproduction

The patterns of spawning and recruitment in Hawaiian reef fishes are distinctly seasonal. In a comprehensive review of the spawning and recruitments of Hawaiian fishes, Walsh (1987) concluded that overall spawning activity peaked in the springtime. Spawning was at a minimum during September–October and at low levels in the winter months (except for a few species, i.e., Watson & Leis 1974, Lobel 1978, Ross 1982, Walsh 1987, this study). This pattern is so far evident among both endemic and widely-distributed species.

Coordination of environmental and reproductive cycles in fishes can be achieved by proximate timing factors which are regularly reoccurring environmental events. These events can elicit specific

responses in the physiological status of the animal. Daylength and temperatures are common stimuli for fish (review by Scott 1979). However, it is probably the spatial-temporal interplay of the proximate stimuli with variables affecting larval survival and recruitment, that ultimately achieve regulation of reproductive cycles. Walsh (1987) argued that the annual variations of peak spawning and recruitment periods in Hawaii were primarily a function of daylength and temperatures, whereas he dismissed the possible significance of ocean current variability in influencing the evolution of these periods.

Daylength and temperatures may be the proximate causal factors involved, and the ultimate causal factor may be the seasonal pattern of ocean currents which affect survival of larvae and recruitment (e.g. Lobel & Robinson 1983). This is not to say, however, that there is not a high rate of loss of larvae by current advection in all seasons. The drift-bottle data suggest, however, that the probability of loss of surface drifting larvae from the Hawaiian islands is lowest during the season of maximum spawning and recruitment.

The hypothesis that ocean current patterns which affect distributions of larvae, also ultimately influence coastal marine fish spawning periods has been most clearly substantiated for Atlantic herring. Iles & Sinclair (1982) showed that the number of genetically distinct herring stocks was determined by the number of distinct, geographically stable retention areas of larvae. The spawning times of the different stocks differed substantially and corresponded in each case to the occurrence of local hydrographic conditions which created geographically stable retention mechanisms (Iles & Sinclair 1982). This hypothesis has been further corroborated by a recent study of reef corals showing localized recruitment of planktonic larvae as a function of a specific spawning period and the seasonality of ocean currents affecting larval dispersal (Sammarco & Andrews 1988).

### *Seasonal oceanography*

The time of peak reproduction in Hawaii occurs during the season of highest wind velocities. In

Hawaiian waters, the wind field is thought to be a significant factor in generating ocean eddies (see below). These eddies have the potential for entrainment and retention of larvae and their food resources (e.g. Lobel & Robinson 1986).

The kinematics and dynamics of a mesoscale eddy field may compensate for the otherwise negative impact of wind induced turbulence on survival of fish larvae. Lasker's (1981) 'stable ocean' hypothesis states that survival of fish larvae is greatest when the upper mixed layer of the ocean is in a stable (nonturbulent) state. This stable state is achieved during prolonged periods of slack wind conditions. Increased survival of larvae of the northern anchovy, *Engraulis mordax*, off southern California was significantly correlated (linear) with the frequency of calm, low wind speed periods during the spawning season (Peterman & Bradford 1987). Lasker's hypothesis attributes increased survival of larvae to the effect of calm winds which permit maintenance of concentrated patches of larval food. In Hawaiian waters, the presence of eddies generated during the highest wind conditions may provide concentrated patches of larval food plus the benefit of entrainment near the islands.

The seasonal patterns of the large scale ocean flow around the Hawaiian archipelago were defined by Barkley et al. 1964. Flow to the northwest and parallel to the archipelago prevailed from January through May (Fig. 7). A shift in currents may begin in June with the flow becoming oriented more perpendicular to the archipelago (Barkley et al. 1964). This shift is correlated with changes in strength of the trade wind system (Barkley et al. 1964). Seckel (1962) described the oceanographic climate as the annual and interannual movement of the southern boundary of the North Pacific central water through the islands (see also Seckel 1985). The North Pacific central water has higher salinity than displaced waters (Seckel 1962). This water mass can be displaced north-southward. The boundary usually lies just south of the islands in the fall and winter, and within or north of the islands during spring and summer (Seckel 1962). The seasonal and geographic patterns of recruitment of lobster larvae throughout the archipelago correspond to the movements of the North Pacific cen-



tral water mass (MacDonald 1985). Boundary displacement was reflected by the salinity measured at Koko Head, Oahu (Seckel & Young 1971). Lower salinities occurred in spring-summer and higher salinities were found in fall-winter. However, in some years this North Pacific water mass appeared stationary and encompassed the islands, and in other years it did not appear at all (Seckel 1972). Further suggestive evidence of a seasonal change in circulation patterns is to be found in the charts of mean dynamic topography by Wyrski (1975). These charts show a clear pattern of a closed gyre scale circulation encompassing the Hawaiian archipelago during March–April. This feature was absent in the dynamic topography during November–December, which showed the flow to the islands from the northwest and away from the islands to the west-southwest. This southwestern current eventually merges with the North Equatorial Current (Jones 1968).

Ocean eddies occur at all times of the year in Hawaiian waters except during periods of slack wind conditions (Patzert 1969, Chopra 1973). When winds are strongest, eddies form off the islands of Hawaii, Oahu and Kauai (Patzert 1969). On an average, winds are strongest from January into May and peak in velocity during April (Wyrski 1974). Patzert (1969) concluded that under the right conditions, eddies: (1) may develop within 10–15 days behind the islands, (2) have average lifetimes of about 65 days, (3) move in a northwesterly direction along the archipelago with mean speeds of about  $6 \text{ cm sec}^{-1}$  and (4) rotate with periods of 4 to 8 days. Lobel & Robinson (1986) showed how one cyclonic eddy remained next to the island of Hawaii for about 70 days. During this time, the cyclonic eddy entrained drifters deployed over reefs. The flow of the eddy dominated coastal currents during its residence next to the island (Robinson & Lobel 1985). The ocean flow windward and north of the island also has a well-defined eddy field that varies seasonally (Roden 1985, Bernstein 1974).

### *Dispersal of larvae and biogeography*

The intriguing aspect of fish spawning patterns in Hawaiian waters is in its possible relationship to survival of larvae and dispersal strategies (Lobel 1978, Lobel & Robinson 1983). The fact that 29% of Hawaiian shore fishes (approximately 460 spp.) are taxonomically recognized as endemic species (Randall 1976, 1980) emphasizes their restricted biogeographic distributions. Given that many of these species have planktonic larva periods lasting two to three months (e.g. Ralston 1981), it is enigmatic how these fishes remain restricted to Hawaiian waters. Furthermore, not all islands around which endemics are found are near each other. Randall et al. (1985) discovered endemic Hawaiian species at Johnston Atoll. Coral species at Johnston Atoll are also predominantly Hawaiian (Maragos & Jokiel 1986). This atoll is situated about 800 km southwest of the nearest reefs in Hawaii and over 1500 km from other reefs to the south and west (Maragos & Jokiel 1986). It is one of the most isolated atolls in the world. It does, however, sit within the domain of the March–April archipelago-sized gyre illustrated in Wyrski (1975).

Two pieces of additional evidence also suggest a path of current drift between the Hawaiian islands and Johnston Atoll. Flow from the main islands to the Atoll was suggested by finding kukui nuts on Johnston Atoll beaches. These nuts had clearly been adrift at sea before being washed ashore (samples have been preserved). Kukui nuts were found during each of three field trips in 1983–1984 (Lobel 1985). The only known sources in the North Pacific are the main Hawaiian islands. Biogeographical data suggesting current flow from Johnston Atoll to the northwest Hawaiian islands were described by Grigg (1981, Grigg et al. 1981). He found populations of a *Acropora* coral living at French frigate shoals and nearby reefs. These *Acropora* coral populations did not appear to be sexually reproductive and, according to Grigg, probably derive from larvae spawned at Johnston Atoll (see also Maragos & Jokiel 1986).

The examples from Johnston Atoll are suggestive of both (1) the dispersal capabilities of Hawaiian fish larvae and, (2) ocean current patterns which

unite the Hawaiian Islands and Johnston Atoll. These ocean current patterns may vary with long term averaged annual periodicity. Genetic evidence supports the view that larvae of some reef fish species are even more widely dispersed and that survival is frequent enough to maintain gene flow between the eastern and central Pacific regions (Rosenblatt & Waples 1986). Larvae of these kinds are known to survive at sea over long distances (Leis 1983, 1984). Some fishes can apparently prolong their pelagic life past the postlarval stages, even developing maturing gonads and adult body shape. This striking occurrence was shown for a large group of *Ctenochaetus strigosus* in the Indian Ocean (Pillai et al. 1983).

The spawning seasonality of shore fishes in Hawaii did not differ distinctly between endemic and pan-tropical Pacific species. Oceanographic evidence supports the hypothesis that the timing of reproduction is significant to the dispersal of larvae and, consequently, the maintenance of island fish populations in Hawaii. This provides a mechanism for the evolution of endemism among those lineages which do not have an influx of larvae from other regions. Considering that Hawaiian populations of species with broad geographic distributions also spawn when most endemics do, suggests that this reproductive season is also influential in survivorship of larvae.

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